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TAXONOMY OF *HETEROTHECA* SECT. *HETEROTHECA* (ASTERACEAE: ASTEREAE) IN MÉXICO, WITH COMMENTS ON THE TAXA OF THE UNITED STATES

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ABSTRACT

Four species are recognized in *Heterotheca* sect. *Heterotheca*, all of which occur in México: *H. grandiflora* Nutt., *H. subaxillaris* (Lam.) Britt. & Rusby, *H. inuloides* Cass. (with three varieties), and *H. leptoglossa* DC. *Heterotheca inuloides* and *H. leptoglossa* are endemic to México, and a new variety restricted to Oaxaca and Puebla is described: **H. inuloides** var. **viridis** *var. nov.* Significant variation also occurs within *H. subaxillaris*, but in a study of the species over its entire range, it has not been possible to recognize meaningful patterns so that even varietal names could be consistently applied. A key to the species is provided as well as discussions of variation and a distribution map for the Mexican taxa.

KEY WORDS: *Heterotheca*, Asteraceae, Astereae, México

Heterotheca sect. *Heterotheca* was monographed by Wagenknecht (1960), who recognized seven species, and it was the subject of further biosystematic study and comments by Harms (1965a; 1968). The generalized distribution map presented by Harms (1965a) for the members of the *H. subaxillaris* (Lam.) Britt. & Rusby complex was based primarily on the discussion and cited specimens of Wagenknecht.

Within the genus, plants of sect. *Heterotheca* are characterized primarily by their dimorphic achenes. The disc achenes are compressed, strigose to sericeous, and with a well developed pappus, typically including 1-3 series of long barbellate bristles and a much shorter, outer series of bristles or scales; the ray achenes are 3 angled, smaller, glabrous or much less pubescent, and completely epappose or rarely with a few short bristles or a minute corona. Further, all species are taprooted and have stems, leaves, and phyllaries with a vestiture of stipitate glandular hairs and spreading, nonglandular hairs with

osteolate bases, midcauline leaves sessile and clasping, heads in a corymboid capitulescence, and yellow, coiling rays.

In the view of Semple, *et al.* (1980), *Heterotheca* also includes another group of approximately 25 species, sect. *Phyllotheca* (Nutt.) V. Harms. They are separated from sect. *Heterotheca* by their monomorphic achenes, although the ray achenes in sect. *Heterotheca* occasionally produce few to numerous pappus bristles, narrowing the morphological gap between the two sections. Two species are rayless, each of them apparently having been derived independently from taxa of sect. *Phyllotheca*, according to Semple, *et al.* (1988), who nevertheless retained one of the rayless species as the sect. *Ammodia* (Nutt.) V. Harms. In more conservative views (see Semple, *et al.* 1980, for a review), *Heterotheca* has been considered to include two groups primarily endemic to the southeastern United States, both now regarded with good evidence by Semple as separate genera: *Chrysopsis* (no Mexican taxa) and *Pityopsis* (one species ranging into México).

Even though the species of sect. *Heterotheca* have relatively recently been studied, identifications and annotations since then have been highly inconsistent. In contrast to the seven species previously recognized, the present report recognizes only four in the section, two of which encompass significant infraspecific variation. At the most general level, they are divided into a northern group of small headed taxa and a southern group of larger headed taxa. All four of the species occur in México.

Although this study was primarily intended to address the patterns of variation in México, it is based on a survey of plants over the entire range of the section, covering the United States as well, in an attempt to meaningfully apply varietal nomenclature to the Mexican representatives. The ecological summaries below, however, refer only to the Mexican plants. Additional synonyms and information on typology are provided by Wagenknecht (1960). Meiotic chromosome numbers of $n=9$ pairs are known for most of the taxa (as summarized by Harms 1965b, Semple 1977, and as noted below).

KEY TO THE SPECIES

1. Innermost phyllaries (8-)9-12 mm long; plants of south central México (3)

1′ Innermost phyllaries 5-9 mm long; plants of northern México and the United States ..... (2)

2. Upper cauline leaves usually at least slightly subclasping to not at all clasping; innermost phyllaries 5-8 mm long; ray achenes usually completely glabrous, disc achenes usually with 1-3 resinous veins; disc corollas glabrous or nearly so; outer pappus strongly developed; herbage drying green ..... *H. subaxillaris*

2′ Upper cauline leaves not clasping; innermost phyllaries 7-9 mm long; the ray achenes minutely strigose at least on the angles, commonly on the faces as well, the disc achenes usually without resinous veins; the disc corollas prominently hairy on the throat; the outer pappus weakly developed; herbage drying dark green to blackish green *H. grandiflora*

3. Perennials or biennials; phyllaries purple at the very apices, the outer 2-3 series with vestiture mostly restricted to the distal half, sparsely glandular to nearly eglandular, with appressed to ascending apressed, relatively thin based, nonglandular hairs along the midregion ..... *H. leptoglossa*

3′ Annuals or biennials; phyllaries either strongly purplish on the tips, margins, and midregions or not at all purplish, the outer 2-3 series with prominent vestiture from base to apex, with thick based, stipitate glands and spreading, thick based nonglandular hairs, or nonglandular hairs commonly absent in var. *rosei* ..... *H. inuloides*

1. *HETEROTHECA GRANDIFLORA* Nutt.

Heterotheca grandiflora Nutt., Trans. Amer. Philos. Soc. 2 7:315. 1840. TYPE: UNITED STATES. California: near Santa Barbara, [1836], *Nuttall s.n.* (PH, not seen).

Annuals to biennials or short lived perennials; stems and leaves sparsely to densely hispid pilose, the herbage with a strong tendency to dry with a pronounced dark cast. Cauline leaves narrowed to a sessile or subsessile, nonclasping, attenuate base, at least on the upper stems. Phyllaries with only glandular hairs, usually purple tipped, the innermost 7-9 mm long. Ray achenes minutely strigose at least on the angles and commonly on the faces as well; pappus with a weakly developed outer series of scales or bristles. Chromosome number, $n=9$ pairs.

Baja California Norte, Sonora, California, southern Arizona; commonly in disturbed sites, sandy soil, dunes, grasslands, chaparral; 3-50(-1200 in the US) m; (May-)June-October(-January).

Heterotheca grandiflora appears to be strongly genetically isolated from *H. subaxillaris*, which is distributed from its native range in the eastern United States westward to California, where it co-occurs with *H. grandiflora*. It is possible that gene flow has occurred from *H. grandiflora* to *H. subaxillaris* (see comments following *H. subaxillaris*), but there is no evidence, however, that the reverse might be true. The strongly darkening pigments do not occur in any other taxa of the section.

2. *HETEROTHECA INULOIDES* Cass.

Heterotheca inuloides Cass., Dict. Sci. Nat. 51:460. 1827. TYPE: MÉXICO. without other data (Probable holotype: FI–Herb. Webbianum *ex* Herb. Desfontaines, GH photo!). According to Cassini, this plant was said by Desfontaines to have originated in México, sent by de Candolle from Geneva to the Jardin du Roi (presumably in Paris). The sheet at FI was annotated in Cassini's hand as "*Heterotheca inuloides*, H. Cass." There is in G-DC (fiche!) a very similar specimen noted as from "J. de Paris 1828" that is possibly a duplicate of the type.

Annuals, biennials, or perennials; stems sparsely to moderately hispid-pilose. Lower leaves petiolate or epetiolate, coarsely serrate, the upper becoming entire, sessile, usually at least subclasping. Phyllaries with a dense vestiture of stipitate glands, on the outer phyllaries these distributed from the base to apex, also densely hirsute-pilose in two varieties with long, nonglandular hairs, but commonly lacking nonglandular hairs in var. *rosei*, the innermost phyllaries (8-)9-12 mm long. Ray achenes usually minutely but prominently strigose on the faces and angles, sometimes glabrous; pappus with a prominent outer series of scales or bristles, these sometimes weakly developed.

Key to the varieties

1. Outer phyllaries densely hispid-pilose from base to tip with spreading to spreading ascending, nonglandular hairs .....(2)

1′ Outer phyllaries without nonglandular hairs or the nonglandular hairs present mostly on the distal third .....var. *rosei*

2. Phyllaries distinctly purplish at least at the apices and commonly along the distal margins and midregion as well, with thick based, nonglandular trichomes .....var. *inuloides*

2′ Phyllaries completely without purple coloration, with relatively thin based nonglandular trichomes .....var. *viridis*

2a. *HETEROTHECA INULOIDES* Cass. var. *INULOIDES*

Chromosome number, $n=9$ pairs.

Nuevo León, Durango, Zacatecas, San Luis Potosí, Hidalgo, Veracruz, Colima, Michoacán, México, Tlaxcala, Puebla; roadsides, fields, openings in pine-oak or pine woodlands; 2000-3000 m; (May-)August-November(-December).

Plants of several scattered collections from far outside its main range must be identified as var. *inuloides*: Nuevo León: Dulces Nombres, 12 Aug 1948, *Meyer & Rogers 2951* (GH). San Luis Potosí: region of S.L.P., 1878, *Parry & Palmer 372* (GH). And as noted by McVaugh (1984), other populations with var. *inuloides*-like phyllaries occur well within the range of var. *rosei*, in the areas of northeastern Nayarit, southeastern Durango, and adjacent Zacatecas. To show their location, these are mapped (Map 1) as var. *inuloides*, although field study may prove these to be variants within more *rosei*-like populations. Further, plants that might be interpreted as intermediate between var. *inuloides* and var. *rosei* occur in the vicinity of Uruapan and Tancitaro, Michoacán, but these are mapped as var. *rosei*.

2b. *HETEROTHECA INULOIDES* Cass. var. *ROSEI* Wagenk.

Heterotheca inuloides Cass. var. *rosei* Wagenknecht, Rhodora 62:69. 1960. TYPE: MÉXICO. Jalisco: sandy soil, grassland and roadsides, 30 mi E of Guadalajara, 25 Jul 1956, *B.L. Wagenknecht 2846* (HOLOTYPE: KANU!).

In addition to the paucity or complete lack of nonglandular hairs, the phyllaries of var. *rosei* usually are completely lacking in purple coloration, they are more densely stipitate glandular than in var. *inuloides*, and the glands usually have thicker stipes. Judging from their more slender taproots, these plants also tend to be more short lived than those of the two eastern varieties of *Heterotheca inuloides*. Chromosome number, $n=9$ pairs.

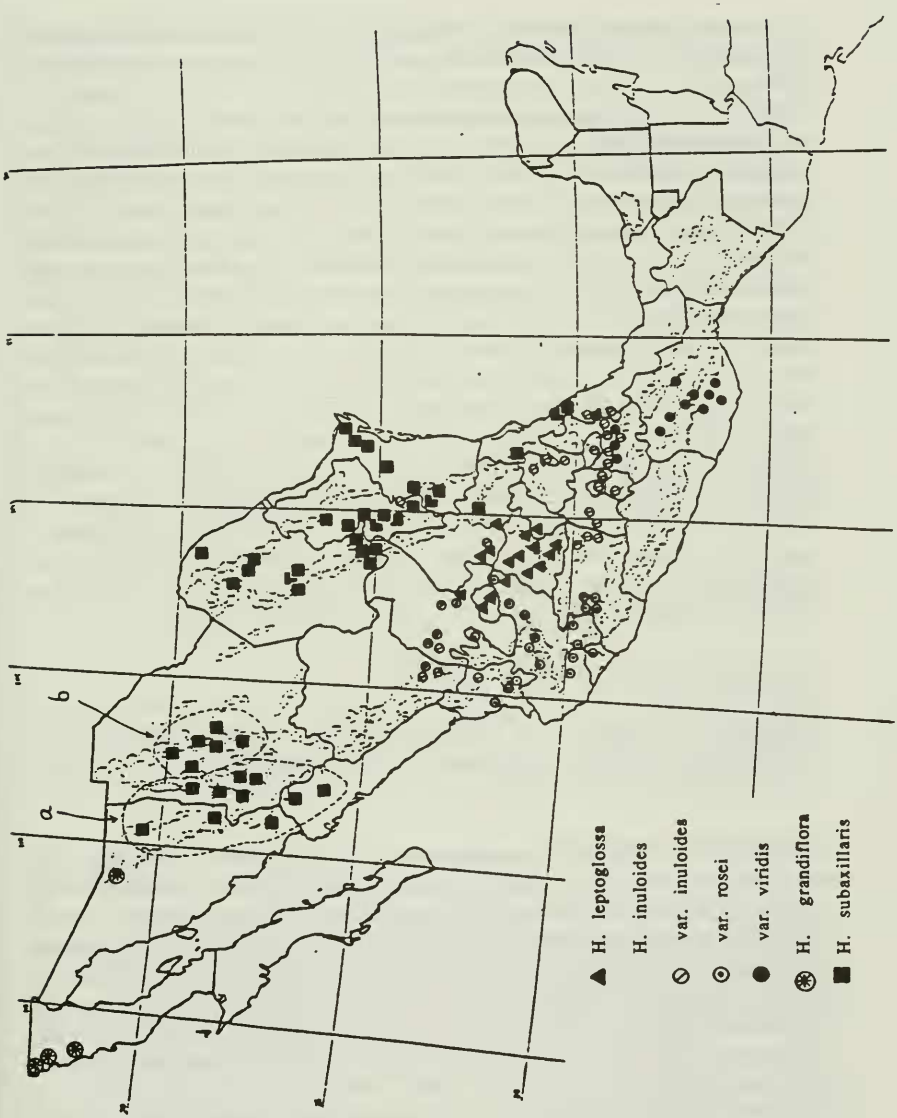
Durango, Zacatecas, Nayarit, Jalisco, Michoacán, Colima; matorral, shrublands, oak-juniper to pine-oak and pine woodlands, roadsides and other disturbed sites, pond edges; 1200-2400 m; (March-)June-November.

2c. *HETEROTHECA INULOIDES* Cass. var. *VIRIDIS* Nesom, *var. nov.*

Heterotheca inuloides Cass. var. **viridis** Nesom, *var. nov.* TYPE: MÉXICO. Oaxaca: Distrito del Centro, Monte Alban, 1850 m, 14 Oct 1932, *C. Conzatti 4794* (HOLOTYPE: LL!; Isotype: MEXU).

A *H. inuloides* Cass. var. *inuloides* differt phyllariis absque pigmento purpurato ac trichomatibus tenuioribus ad bases longioribusque.

These plants are similar to those of var. *inuloides* in their phyllaries with a densely hirsute-pilose vestiture but consistently different in their complete lack of purple coloration and the longer nonglandular trichomes with thinner bases. Intermediates between the two taxa occur in northern Puebla and along the adjacent border with Veracruz. Chromosome number, $n=9$ pairs.



Map 1. Geographic distribution of the taxa of *Heterotheca* sect. *Heterotheca* in México.

Veracruz, Puebla, Oaxaca; openings in oak-juniper and pine-oak woodlands, roadsides and other disturbed sites; 1550-2300 m; June-November (-February).

Representative collections examined: MÉXICO. Oaxaca: Valley of Oaxaca, 19 Apr 1896, *Conzatti 125* (GH); Km 58 S of Oaxaca on road to Puerto Escondido, 14 Aug 1975, *Davidse 9623* (LL); between Oaxaca and Puerto Escondido, 8 km S of Sola de Vega, 25 Jun 1986, *Diggs, et al. 4005* (NY); 20 mi S of Nochixtlan along rte 190, 1 Feb 1960, *King 2515* (TEX) (voucher for chromosome count of $n=9$, as annotated by Ellison, apparently previously unreported); ca. 40 mi SE of Oaxaca, 15 Jun 1960, *King 2897* (TEX) (voucher for chromosome count of $n=9$ pairs [Turner, *et al.* 1961]); 15 km SE of Miahuatlán, 6 Jul 1969, *Marcks & Marcks 1048* (LL); 19 mi W of Oaxaca along rte 190, 15 Aug 1961, *Powell & Edmondson 703* (TEX); 11 km N of Ixtlan, 17 Sep 1965, *Roe & Roe 1989* (LL); 33 km NE of Cuajimoloyas, 14 May 1983, *Torres 2891* (TEX). Puebla: Supercarretera México-Puebla, 24 Apr 1966, *Boege 66* (GH); Orizaba, 1829, *Botteri 799* (GH); 1 mi E of Hwy 125, N of San Salvador on road to Tlachichuca, 7 Jun 1983, *Dorr 2673* (TEX); 5 mi E of Tlahuapan along rte 190, 24 Jan 1960, *King 2236* (TEX); W of San Martín Texmelucan, 1 Aug 1953, *Manning & Manning 53689* (GH); 3 km E of center of San Nicolas Buenos Aires, 7 Sep 1986, *Nee & Soule 33040* (TEX). Veracruz: S of Totalco, 27 Aug 1968, *Ramos 269* (GH).

3. *HETEROTHECA LEPTOGLOSSA* DC.

Heterotheca leptoglossa DC., *Prodr.* 5:317. 1836. TYPE: MÉXICO. [Edo.] Guanajuato: León to Guanajuato, 1827, *Mendez s.n.* (HOLOTYPE: G-DC fiche!; Isotype: GH).

Perennials. Phyllaries linear-lanceolate, 0.5-0.7(-1.0) mm wide, the innermost 9-11 mm long, without scarious margins, purple at the very apices, nearly eglandular to sparsely sessile glandular or the glands short stipitate near the phyllary apex, sparsely strigose in the midregion with appressed to appressed ascending nonglandular hairs. Ray achenes commonly minutely strigose on the angles and faces, sometimes hairy only on the angles or still less commonly completely glabrous; outer pappus of strongly developed, lanceolate scales. Chromosome number, $n=9$ pairs (reported as *Heterotheca inuloides* by Turner & Johnston 1961).

Zacatecas, Aguascalientes, San Luis Potosí, Jalisco, Guanajuato, Querétaro; roadsides and other disturbed sites, brushlands; 1750-2350 m; July-December (-January).

Heterotheca leptoglossa was recognized by Wagenknecht (1960) as a distinct species, but he cited only two collections (other than the type) from the geographical area of the species as recognized here. He added, however,

citations of other collections from Chihuahua, Sinaloa, and Sonora, all recognized here as *H. subaxillaris* (Map 1, region "a"). McVaugh (1984) included *H. leptoglossa* within his concept of *H. inuloides* var. *rosei.*

This taxon might reasonably be considered as a fourth variety of *Heterotheca inuloides*, but it appears to be genetically isolated from both var. *inuloides* and var. *rosei.* The former is mostly contiguous with it in geographic range and the latter is partially sympatric (Map 1). *Heterotheca leptoglossa* is more similar to var. *rosei* in its very sparsely hairy phyllaries, but the former differs in its more strongly woody taproots (and presumably longer duration) and phyllaries that are purple tipped and less densely glandular with relatively thin stiped glands. Further, the nonglandular hairs are usually appressed in orientation, in contrast to the spreading-erect ones of var. *rosei.*

4. *HETEROTHECA SUBAXILLARIS* (Lam.) Britt. & Rusby

Heterotheca subaxillaris (Lam.) Britt. & Rusby, Trans. New York Acad. 7:10. 1887. BASIONYM: *Inula subaxillaris* Lam., *Encycl. Meth. Bot.* 3:259. 1789. TYPE: UNITED STATES. "Carolina," *D. Walter s.n.* (HOLOTYPE: P, not seen).

Heterotheca chrysopsidis DC., *Prodr.* 5:317. 1836. TYPE: MÉXICO. [Coahuila]: Saltillo, Jan 1828, *Berlandier 1830* [*109*] (HOLOTYPE: G-DC fiche!; Isotypes: F!, GH, NY, PH).

Heterotheca latifolia Buckl., Proc. Acad. Nat. Sci. Philadelphia 13:459. 1862. TYPE: UNITED STATES. Texas: Llano Co., *S.B. Buckley s.n.* (PH, not seen). *Heterotheca subaxillaris* (Lam.) Britt. & Rusby var. *latifolia* (Buckl.) Gandhi & Thomas, Sida, Bot. Misc. 4:110. 1989.

Heterotheca latifolia Buckl. var. *arkansana* Wagenk., Rhodora 62:105. 1960. TYPE: UNITED STATES. Arkansas: Logan Co., Magazine Mountain, 10 Sep 1930, *D.M. Moore 30142* (HOLOTYPE: TEX!).

Heterotheca latifolia Buckl. var. *macgregoris* Wagenk., Rhodora 62:103. 1960. TYPE: UNITED STATES. Kansas: Morton Co., 9 mi N of Elkhart, bluffs along Cimmaron River, dry sandy prairie, 27 Aug 1951, *R.L. McGregor 5163* (HOLOTYPE: KANU!).

Heterotheca psammophila Wagenk., Rhodora 62:76. 1960. TYPE: UNITED STATES. Arizona: Yavapai Co., 1 mi S of Sedona, 23 Aug 1957, *B.L. Wagenknecht 4824* (HOLOTYPE: KANU not seen).

Heterotheca subaxillaris (Lam.) Britt. & Rusby var. *petiolaris* Benke, Rhodora 30:201. 1928. TYPE: UNITED STATES. Texas: [Galveston Co.], Galveston, 12 Mar 1928, *H.C. Benke 4585* (HOLOTYPE: F!).

Heterotheca subaxillaris (Lam.) Britt. & Rusby var. *procumbens* Wagenk., Rhodora 62:75. 1960. TYPE. UNITED STATES. Alabama: Mobile Co., flattish dunes, ca. 1 mi SW of Dauphin Island Post Office, *R.M. Harper 3801* (HOLOTYPE: GH; Isotypes: F!, NY, PH, US).

Annuals to short lived perennials. Upper cauline leaves ovate lanceolate to oblong, with a sessile or subsessile, commonly cordate, subclasping base, but sometimes not at all clasping. Phyllaries lanceolate, the innermost 5-8(-9) mm long, purple at the apices or without purple pigments, sparsely to densely glandular, usually sparsely to moderately invested with nonglandular trichomes but sometimes only glandular. Ray achenes usually completely glabrous, rarely slightly and minutely strigose on the angles; outer pappus of strongly developed, lanceolate scales. Chromosome number, $n=9$ pairs.

Sonora, Chihuahua, Sinaloa, Coahuila, Nuevo León, Tamaulipas, San Luis Potosí, Veracruz, widely distributed from coast to coast in the United States, primarily in the southern half of the country; in a variety of habitats, often disturbed, from beach dunes to *Larrea* desert to pine woodlands; (0-)1200-2500 m; July-December(-February).

Within what is considered here as a single, variable species, Wagenknecht (1960) treated *Heterotheca subaxillaris* (with 2 varieties), *H. latifolia* Buckl. (with 3 varieties), *H. psammophila* Wagenk., and *H. chrysopsidis* DC. Before that, Shinners (1951) had accepted *H. latifolia* as a good taxon with the caveat that it was probably only varietally distinct from *H. subaxillaris*, "the southeastern representative of this species." The status of the Mexican *H. chrysopsidis* had never been evaluated, and *H. psammophila* had not previously been recognized. Characters used to delimit these taxa have included duration (as surmised from the taproot thickness), plant height, stem width, length of trichomes on the stems and leaves, petiole length of lower cauline leaves, size, shape, and insertion of upper cauline leaves, toothing of leaf margins, shape of the capitulescence, head size (including phyllary, disc corolla, and pappus length), degree of investment of phyllaries with glandular and nonglandular trichomes, and the pattern of pigmentation in the phyllaries.

Attempts to characterize taxa at any level within the *Heterotheca subaxillaris* complex must be based on the supposition that geographic patterns can be identified, but among what seem to be shifting and variable constellations of morphological features, I have not been able to discover patterns that would allow a consistent application of names at even varietal rank. Harms (1968, p. 9) ventured that perhaps the "entire complex should still be accepted as a single, polymorphic, polytypic species," and Cronquist (1980) apparently took the same conservative view as presented in the present study, although he did not list synonyms of what he considered to be the widespread *H. subaxillaris*. Geographic trends can be observed in this species, and plants can often be

identified as having originated in certain geographic areas, but in my opinion, plants occurring in broad areas of intergradation are significantly more numerous than those that have been given names and that are said to have a distinctive combination of traits. In this, my view seems to be very near that of Semple (1990, p. 226) with regard to plants of certain species of sect. *Phyllotheca*, who regards them as "morphotypes," " ... sometimes semidistinct regional 'races' that grade into each other to such an extent that continued recognition cannot be justified ...." Whoever may choose to recognize segregate taxa within the *H. subaxillaris* complex will be challenged to present more than simple diagnoses and taxonomic combinations to justify their decisions.

What has been considered typical *Heterotheca subaxillaris* (var. *subaxillaris* or var. *procumbens*) occurs in sandy habitats along the coast of the eastern United States to central México. These plants are said to be distinguished from *H. latifolia* by their procumbent or at least less than erect habit, merely scabrous stems and leaves, thicker leaves, and more densely hirsute-villous hairs on the phyllaries. Nearly identical plants, however, are found in sandy habitats far inland within the range of *H. latifolia*, and plants with none of the putatively diagnostic features of typical *H. subaxillaris* are commonly collected in coastal and near coastal sites. Further, Burk (1961), in a study apparently little appreciated by some systematists, demonstrated that plants of *H. subaxillaris* are phenotypically highly plastic in features of habit, vestiture, and leaf morphology. He transplanted sets of North Carolina plants from a barrier island (var. *procumbens*) and from an inland habitat (*H. latifolia*) to a common garden on the piedmont, where they "developed into virtually identical sets of plants." Using cloned individuals, he also observed that vestiture was significantly modified depending on the season and whether the plants were grown in a greenhouse or outdoors. Burk concluded that it was preferable to "retain the former concept of *H. subaxillaris* as a single, highly variable species." Harms (1965a) also documented the ease of environmental modification among plants of *H. subaxillaris*.

Harms (1965a, 1968) noted that he was able to distinguish *Heterotheca latifolia* var. *macgregoris* Wagenk. but that he could not separate it from var. *arkansana* Wagenk. Wagenknecht (1960) separated both of the latter two varieties from typical *H. latifolia* on the basis of their putatively more pilose or velutinous upper leaf surfaces, but I cannot confirm the existence of any morphological features or geographic localization consistent enough to warrant the formal recognition of either taxon. Hatch, *et al.* (1990) have listed (without comment) both var. *arkansana* and var. *macgregoris* as synonyms of var. *latifolia*.

Heterotheca subaxillaris var. *petiolaris* Benke has been considered a synonym of typical *H. subaxillaris* (Burk 1961) and of *H. latifolia* (Wagenknecht 1960). But plants similar to the type of var. *petiolaris* with particularly long petioles and narrowly oblong-lanceolate blades (basal and lower cauline leaves)

are common from Galveston County, Texas, into Tamaulipas of northeastern México and appear to represent a morphotype outside of both *H. subaxillaris* and *H. latifolia*, as conceived of by Wagenknecht. In any case, "var. *petiolaris*" intergrades with other morphotypes of the same region and cannot be consistently distinguished from them.

As noted by Wagenknecht, plants of *Heterotheca chrysopsidis* (from southern Coahuila and adjacent Nuevo León) are slightly longer lived, shorter in stature, have petiolate, prominently thickened (much like coastal variants) leaves with broadly ovate blades, and the pappus tends to be deep reddish brown. These features are most pronounced in plants from the gypseous areas of Nuevo León. Nevertheless, I have found it impossible to regard these traits as anything but tendencies, since many plants from the same area are identical with those that are common in central Texas, and the distinctive traits disappear gradually northward through Coahuila.

Heterotheca psammophila was recognized by Wagenknecht from Arizona, southwestern New Mexico, trans-Pecos Texas, and northern México as a taxon with particularly large leaves, large heads, and highly glandular phyllaries. The plants do seem to have consistently larger leaves, but plants with similar leaves grade eastward across a wide area and sometimes appear in populations of central Texas, Oklahoma, and Kansas. Further, in Arizona and western New Mexico, while some individuals produce heads that are among the largest in the species (innermost phyllaries 7-9 mm long), other large leaved plants in the same area commonly produce small heads (innermost phyllaries 5-7 mm long). There is no consistent distinction in the degree of glandularity, and in the United States, no consistency in the presence or absence of nonglandular hairs.

In contrast, there does appear to be a degree of isolation between two weakly differentiated "morphotypes" of *Heterotheca subaxillaris* in the mountains of northwestern México. Indeed, this is the only "real" boundary I have been able to discover in the *H. subaxillaris* complex. Plants of region "a" (Map 1) have phyllaries with purple tips, without non-glandular hairs, and the innermost are 6-8(-9) mm long. To the east in central Chihuahua (region "b"), the phyllaries usually lack purple tips, almost always produce nonglandular hairs, and the innermost are 5-6 (-7) mm long. The plants of region "a" might justifiably be regarded as a separate variety, presumably corresponding to *H. psammophila*, were it not for the apparent complete intergradation in Arizona of these "*psammophila*-like" plants with more typical *H. subaxillaris*.

The occurrence of dense glandularity and relatively large heads in the western part of the range of *Heterotheca subaxillaris* prompts the speculation that these features may have appeared in response to the input of genes from *H. grandiflora*.

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LITERATURE CITED

Burk, C.J. 1961. Environmental variation in *Heterotheca subaxillaris*. Rhodora 63:243-246.

Cronquist, A. 1980. Asteraceae. *Vascular Flora of the Southeastern United States*, vol. 1. Univ. North Carolina Press, Chapel Hill.

Harms, V.L. 1965a. Biosystematic studies in the *Heterotheca subaxillaris* complex (Compositae: Astereae). Trans. Kansas Acad. Sci. 68:244-257.

_____. 1965b. Cytological evidence supporting the merger of *Heterotheca* and *Chrysopsis*. Brittonia 17:11-16.

_____. 1968. Nomenclatural changes and taxonomic notes on *Heterotheca*, including *Chrysopsis*, in Texas and adjacent states. Wrightia 4:8-20.

Hatch, S.L., K.N. Gandhi, & L.E. Brown. 1990. *Checklist of the Vascular Plants of Texas*. Texas A & M Agric. Expmt. St., College Station.

McVaugh, R. 1984. *Heterotheca*. Flora Novo-Galiciana 12:505-508. University of Michigan, Ann Arbor.

Semple, J.C. 1977. Cytotaxonomy of *Chrysopsis* and *Heterotheca* (Compositae: Astereae): a new interpretation of phylogeny. Canad. J. Bot. 55:2503-2513.

_____. 1990. Neotypification of *Amellus villosus*, the identity of a Bradbury collection, and typification of some other goldenasters (Compositae: Astereae). Brittonia 42:221-228.

_____, V. Blok, & P. Heiman. 1980. Morphological, anatomical, habit, and habitat differences among the goldenaster genera *Chrysopsis, Heterotheca* and *Pityopsis* (Compositae - Astereae). Canad. J. Bot. 58:164-171.

Semple, J.C., C. Leeder, C. Leuty, & L. Gray. 1988. *Heterotheca* sect. *Ammodia* (Compositae: Astereae): A multivariate study of *H. oregona* and specimens of Brewer's (Golden)aster. Syst. Bot. 13:547-558.

Shinners, L.H. 1951. The North Texas species of *Heterotheca*, including *Chrysopsis* (Compositae). Field & Lab. 19:66-71.

Turner, B.L., W.L. Ellison, & R.M. King. 1961. Chromosome numbers in the Compositae. IV. North American species with phyletic interpretations. Amer. J. Bot. 48:216-223.

Turner, B.L. & M. C. Johnston. 1961. Chromosome numbers in the Compositae III. Certain Mexican species. Brittonia 13:64-69.

Wagenknecht, B.L. 1960. Revision of *Heterotheca* section *Heterotheca* (Compositae). Rhodora 62:61-76.

_____. 1960. Revision of *Heterotheca* section *Heterotheca* (Compositae). Rhodora 62:97-107.